Effect of Temperature on Development and Population Parameters of *Copitarsia decolora* (Lepidoptera: Noctuidae)

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ABSTRACT The objective of this study was to evaluate the effect of temperature on survival, development, and reproduction of *Copitarsia decolora*. Both linear and nonlinear models were used to model temperature-dependent development and population growth for *C. decolora* reared on asparagus and artificial diet. We used @Risk Software to bootstrap model parameters so that variability in observations could be incorporated into model predictions. *C. decolora* eggs required ≈69 DD to complete development with a base temperature of 7.8°C. *C. decolora* developed through four to six instars depending on temperature and food source. Development of larvae from neonate through prepupa required 341.4 DD above a base of 7.3°C on asparagus, whereas 254.5 DD were needed on artificial diet, where the base temperature was 7.7°C. Pupae required ≈236 DD (base temperature 8.2–8.4°C) to develop when reared on asparagus or artificial diet. Female moths laid significantly more eggs at 14.6 and 20.1°C than at higher or lower temperatures. Survival of individuals to the adult stage increased from 71% at 9.7°C to 93% at 24.9°C. Survival fell off rapidly to 25% at 29.5°C. The generation time was the shortest at 29.5°C; however, only 25% of females survived to the adult stage, fecundity was low, and only 53% of the eggs hatched. The capacity for increase, r_c, was low at 9.7°C, peaked at 25.7°C, and declined as temperature increased. We estimated that populations on asparagus would not develop at temperatures >31.3°C or <6.9°C. We show the importance of estimating a range of values for base temperature and degree-days by conducting a preliminary pathway analysis that incorporates the effect of temperature on egg hatch.

KEY WORDS *Copitarsia*, degree-days, Noctuidae, temperature-dependent development

MOTHS IN THE GENUS *Copitarsia* Hampson (Lepidoptera: Noctuidae) are generally found from Mexico south through South America. The larvae have five to six instars (Arce de Hamity and Neder de Roman 1993, Lopez-Avila 1996) and reach a length of ≈2–4 cm. The larvae tend to be green in color, but green, black, and gray phases occur that vary with habitat and crops attacked (Lopez-Avila 1996). *Copitarsia* species pupate in the soil and emerge as gray or brown moths that are difficult to distinguish from other noctuids. Literature reports suggest that *Copitarsia* species are multivoltine through much of the range (Artigas and Angulo 1973, Liberman-Cruz 1986, Arce de Hamity and Neder de Roman 1992). *Copitarsia* tend to be highly fecund, laying between 500 and 1,600 eggs per female depending on the species and food source (Velasquez Z. 1988, Arce de Hamity and Neder de Roman 1992, Rojas and Cibrian-Tovar 1994, Larrain S. 1996). Polyphagy also seems to be common among members of this genus.

Based in part on the high fecundity, multivoltinism, and polyphagy, members of the genus *Copitarsia* Hampson (Lepidoptera: Noctuidae) are of regulatory concern to the United States. They are frequently intercepted on produce and cut flowers at U.S. ports of entry and are considered actionable, quarantine pests (USDA 2003). If *Copitarsia* eggs or larvae are found in a shipment, the commodity must be treated with pesticides, destroyed, or returned to the country of origin (USDA 2003). Several risk assessments of *Copitarsia* species have concluded that these are high-risk pests (Cave and Redmond 1997a, b, USDA 1997); however, a comprehensive risk assessment of the genus concluded that sufficient data were not available to address many risk elements (Gould et al. 2000, Venette and Gould 2005). In particular, these assessments questioned the ability to predict the likelihood that *Copitarsia* could establish in the United States. When initial models of the potential geographic range of the genus *Copitarsia* in the United States (Gould et al. 2000) were developed, detailed data on response of these insects to climatic conditions such as temperature and soil moisture were not available. Climate matching, based on the known distribution of *Copitarsia*, was the only option. Characterizing the geographical distribution with any accuracy was difficult because many *Copitarsia* species are recorded from the western coast of South America, where the Andes Mountains rise steeply over short distances. Climate

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predictions for individual species also were impossible given the confusion in the taxonomy of the genus (Simmons and Pogue 2004). The lack of accurate data on which to model the response of *Copitarsia* to temperature was identified as an important area for future research. This study was undertaken to fill this critical data gap.

The first step toward developing better predictions of risk was to conduct research on a known species. We collected a *Copitarsia* species from asparagus in Ica, Peru, and conducted biological studies on this single species. Recent systematic research (Simmons and Pogue 2004) has allowed us to accurately identify this species as *C. decolora* (Guenée), although this moth had previously been called *C. incommoda* (Walker). *C. decolora* was identified using morphological and molecular methods (R. Simmons, personal communication). Historically, the names *C. incommoda* and *C. turbata* (Herrich-Schäffer) were switched, and *C. turbata* was a synonym for *C. decolora* (Simmons and Pogue 2004).

The objective of this study was to evaluate the effect of temperature on survival, development, and reproduction of *C. decolora.* We used this information to construct a probabilistic development model. The development of predictive phenological models requires an understanding of the relationship between insect development and temperature. Several models have been used to describe the influence of temperature on insect developmental rates (reviewed in Sharpe et al. 1977, Wagner et al. 1984, 1991, Liu et al. 1995, 2002, Wellington et al. 1999). Among the simplest development models is a linear equation relating the inverse of development time to temperature. Such models are useful for characterizing the mean developmental rate within a population but do not accurately describe the variation in this rate among individuals (Wagner et al. 1991). Alternative models based on the distribution of developmental times among individuals have been proposed to more accurately predict when a given fraction of the population will complete development (reviewed in Wagner et al. 1984, 1991). These methods typically use a Weibull function to describe the distribution of development times and then generate a single curve that describes normalized development times (Liu et al. 2002).

Advances in the discipline of ecological risk assessment show the importance of considering the mean and variance when modeling population responses to environmental conditions (Vose 2000). For insects that are not yet known to occur in the United States, such models are useful in predicting the degree of development at different points along one or more potential pathways of introduction. We used the simulation modeling software @RISK (Palisades Corporation, Newfield, NY) to describe the distribution of developmental times for *C. decolora* at each temperature and used bootstrap techniques to develop distributions of base temperatures and degree-day requirements.

Materials and Methods

Colony Initiation and Maintenance. A colony of *C. decolora* was derived from 150 eggs and larvae collected in Ica, Perú, in September 2001. The colony was maintained in a high-security quarantine laboratory (United States Department of Agriculture, Animal and Plant Health Inspection Service Laboratory, Plant Protection and Quarantine) in Bourne, MA. Additional *C. decolora* eggs were collected in January 2003, reared to the adult stage, and added to the colony to introduce fresh genetic stock. Larvae were reared on high wheat germ diet (Bell et al. 1981) in a walk-in environmental chamber at 23°C and 73% RH with a photoperiod of 14:10 (L:D) h. Adults were reared in 18-cm-diameter by 17-cm-high cardboard chambers and provided a liquid diet of orange Gatorade (Gatorade Co., Chicago, IL). In each generation, 10 cages with ≈40 adults each were established as mating chambers by randomly selecting pupae from the colony. Asparagus spears were placed in mating chambers to stimulate egg laying, but the majority of eggs were laid on brown paper lining the chambers. Voucher specimens are deposited in the Lepidoptera collection at the National Museum of Natural History (Smithsonian Institution, Washington, DC).

Temperature-Dependent Egg Hatch. Twenty *C. decolora* eggs on brown paper were placed in each of 10 petri dishes for a total of 200 eggs at each temperature. The eggs were placed in reach-in plant growth chambers (Percival Scientific, Perry, IA) with photoperiods of 14:10 (L:D) h and temperatures set at 5, 10, 15, 20, 25, 30, and 35°C. A Hobo temperature recorder (Onset Computing, Bourne, MA) was placed in each environmental chamber. Average recorded temperatures were used in all calculations. The average recorded temperatures were 5.0, 9.3, 14.3, 20.5, 25.3, 30.1, and 34.5°C, respectively. The eggs were checked daily, and the number of larvae emerging each day was recorded. We discontinued checking the eggs when they became desiccated and collapsed.

Temperature-Dependent Development from Neonate Through Adult. Development of larvae, pupae, and adults was observed in growth chambers at 9.7, 14.6, 20.1, 24.9, 29.5, and 34.5°C. To evaluate development on asparagus, neonate larvae were placed individually in 60-ml plastic cups (Comet P-20) with paper lids. Asparagus was purchased from a local grocery store. Approximately 4 cm of asparagus stem was added to each cup to provide food for larvae. At temperatures >25°C, the asparagus stems were replaced daily because they dehydrated; at lower temperatures, they were replaced every other day. Forty larvae were monitored at each temperature, with the exceptions of 30°C, at which 70 individuals were monitored, and 35°C, at which 50 individuals were tested. Development rate on artificial diet was determined by rearing fifty individuals per temperature. Larvae on artificial diet were reared in the same chambers at the same time as larvae on asparagus. Neonate larvae were placed individually in 60-ml cups (Comet P-20) filled two-thirds full of high wheat germ diet (Bell et al.

1981) and covered with paper lids. All larvae were checked daily, and the developmental stages were recorded. Head capsules or exuviae from molting were located before a molt was recorded.

When larvae became short and c-shaped, they were recorded as having entered the prepupal stage. Pupae were weighed 5 d after pupation, and all individuals continued to be observed daily. The sex of emerged adults was determined, and male-female pairs were placed in 8.5-cm-tall by 8.5-cm-diameter paper canisters for mating and egg laying. Gatorade and asparagus spears were placed in each cage. After oviposition was observed, the male and female were placed in separate cages and monitored daily until death. If males remained with females, we found that the pairs eventually remained locked in copula, and the female could not lay eggs. Every 3 d, the brown paper with the eggs from each female was removed, and fresh paper was provided. The number of eggs each female laid during that 3-d period was recorded. Twenty of those eggs were placed in petri dishes and checked daily to determine the percentage of eggs that were viable.

Data Analysis. Analysis of developmental time, number of instars, pupal weight, adult longevity, and total eggs per female among temperatures and between food sources and sexes (for pupae and adults) were conducted using analysis of variance (ANOVA; PROC GLM; SAS Institute 1990). Multiple comparisons were made using Ryan-Einot-Gabriel-Welsch multiple range tests (SAS Institute 1990). The relationship between the number of eggs laid and pupal weight was estimated using PROC REG (SAS Institute 1990).

Developmental Rate Versus Temperature. The relationship between development and temperature was determined using linear regression (PROC REG; SAS Institute 1990). We attempted to fit the model of Logan et al. (1976), as modified by Lactin et al. (1995), but parameter estimates failed to converge on reasonable values. Developmental rate was linear between 9.3 and 30.1°C for eggs and between 9.7 and 29.5°C for larvae and pupae, yet no eggs hatched and no larvae survived to the pupal stage at 34.5°C. We therefore used only linear models to describe development in relation to temperature.

We conducted traditional analyses by regressing the mean developmental rates versus temperature. This resulted in a single estimate of the base temperature where development begins and one estimate of the number of degree-days required for development for each life stage. We also used Monte Carlo simulation to determine the distribution of estimates of base temperatures and degree-days required for insect development. The first step was to describe the statistical distribution of developmental times for each stage at each temperature using the define distribution function in @RISK software (Palisades Corporation 2001). We estimated statistical distributions rather than empirical distributions because our sample size was small relative to the range of possible outcomes. A logistic distribution was used in all cases because it consistently fit the data best. Using @RISK, we sampled one value from the distribution of developmental rates for each temperature, put the rate values in an output data set, and repeated this process 1,000 times. From the output dataset we ran 1,000 linear regressions and calculated the base temperature and number of degree-days required for development for each iteration. From the resulting distribution of values, we were able to determine the mean and 95% confidence interval (CI) for base temperature and degree-days.

Population Growth. To determine the temperature conditions necessary for positive population growth, we estimated the net reproductive rate (R_0) and the intrinsic rate of population increase (r) at each temperature. We calculated R_0 by multiplying the proportion of female insects that reached the adult stage by the number of viable female eggs produced per female (Southwood 1978). Because *C. decolora* has a 1:1 sex ratio (J.R.G., unpublished data), we assumed that one-half of the eggs were female. An approximate value for population growth rate (the capacity for increase, r_c) can be calculated as $\ln(R_0)/T$, where T is the generation time (in days) or the mean age of females at the birth of female offspring (Southwood 1978).

The relationship between population growth and temperature was examined using nonlinear methods (the model of Logan et al. 1976, as modified by Lactin et al. 1995). Lactin et al. (1995) made two modifications to the Logan model. One modification was to remove a redundant parameter, ψ, and the second was to add the term λ, which allowed the curve to reach the x-axis and allowed for estimation of a base temperature. The advantages of the modified Logan model are that it allows calculation of a maximum temperature, an optimum temperature, and if the four parameter model is used, a base temperature. The four parameter model did not meet the criteria of statistical significance at $\alpha = 0.05$ because of limited degrees of freedom; therefore, we used the three parameter model. Base temperatures were estimated by linear regression of population growth rates on temperatures between 9.7 and 29.5°C, as described above for developmental rates.

To describe the distribution of r_c values at each temperature, we used @RISK to fit statistical distributions to values of r_c calculated for each female. The logistic, Weibull, and log logistic distributions were used depending on which distribution fit the data best. The logistic equation fit the data most consistently among temperatures for the two food types. We used @RISK software to sample from these distributions 1,000 times, outputting values of r_c for each temperature at each iteration. These data were used as input for the modified Logan model using three parameters:

$$R(T) = e^{\rho T} - e^{[\rho T_{max} - (T_{max} - T)/\Delta]}$$

where ρ, T_{max}, and Δ are fitted parameters. T_{max} is the maximum temperature where population growth can occur, and the curve reaches its highest point at $T_{max} - \Delta$. We used PROC NLIN (SAS Institute 1990, method = Marquardt, smethod = golden) to fit the Logan model to each of the 1,000 output data values

Table 1. Mean developmental time of eggs (± SE) and egg hatch (%) when exposed to different temperatures

Temperature (°C)	Number of days to hatch	Percent hatch
5.0	No hatch observed	0
9.3	33.1 ± 1.4	69.5
14.3	12.6 ± 0.7	53.5
20.5	5.2 ± 0.4	61.4
25.3	4.2 ± 0.4	37.6
30.1	3.0 ± 0.2	53.5
34.6	No hatch observed	0

N = 200 per temperature.

of r_c. The results gave us distributions of values for ρ, T_{max}, and Δ. Subtracting Δ from T_{max} gave us estimates of the optimum temperature for population growth. The same output values were used to calculate 1,000 slope and intercept values for linear regression. The base temperature estimates were calculated from the regression formulae.

Results and Discussion

Eggs. The time required for *C. decolora* eggs to hatch ranged from 3.0 ± 0.2 d at 30.1°C to 33.1 ± 1.4 d at 9.3°C (Table 1). Percentage of egg hatch was variable, but it did not seem to be related to temperature (Table 1), except that no hatch occurred at the extreme upper and lower temperatures. *C. decolora* eggs took ≈69 DD to develop with a base temperature of 7.8°C (Table 2), based on regression of mean values. There was little deviation of the mean developmental rates from the regression line (R^2 = 0.991). Simulation modeling using @Risk software predicted the same base temperature and a similar number of degree-days for egg hatch. @Risk modeling predicted a 95% CI of 7.2–8.3°C for the base temperature and a 95% CI of 64.4–72.6 for the number of degree-days required for hatch.

Comparison of our results to other published literature is difficult because of the taxonomic confusion within the genus *Copitarsia.* Larrain (1996), studying *C. turbata* reared on artificial diet in Chile, found that eggs hatched in 6.8 d at 20°C and 75% RH; whereas at 20.5°C, we found that *C. decolora* eggs hatched in 5.2 d. At 25.3°C, our results showed egg hatch after 4.2 d. In contrast, Arce de Hamity and Neder de Roman (1992), studying *C. turbata* reared on lettuce in Argentina, found hatch after 8 d at 24.5°C. The results are clearly different and are possibly caused by misidentification of species in earlier studies or to differences in food source consumed by the parents. Velasquez Z. (1988), studying *C. turbata* reared on onion in Perú, found that eggs hatched in 5.4 d at 20.4°C, which is similar to what we found for *C. decolora.* Arce de Hamity and Neder de Roman (1992) found that changing daylength from 0 to 12 to 24 h changed the number of days for eggs to hatch by 1–2 d. Larrain S. (1996) and Velasquez Z. (1988) did not report the daylength used in their studies.

Larvae. *Copitarsia decolora* developed through approximately six instars at 9.7 and 14.6°C (Table 3)

Table 2. Degree-days and base temperatures for development of *C. decolora* eggs, larvae, pupae, and one generation

Stage	Food	R^2 of linear regression of means	F	Pr > F	Base temperature (regression of means)	Base temperature @Risk model (α; β of logistic)	95% CI for base temperature	Degree-days (regression of means)	Degree-days @Risk model (α; β of logistic)	95% CI for degree-days
Egg	-	0.991	319.7	0.0004	7.8	7.8; 0.149	7.2–8.3	69.1	68.4; 0.141	64.4–72.6
Larva and prepupa	Asparagus	0.995	573.7	0.0002	7.3	7.3; 0.476	5.6–9.0	341.4	337.5; 20.92	261.2–412.5
Larva and prepupa	Artificial diet	0.991	334.4	0.0004	7.7	7.7; 0.380	6.3–9.0	254.5	249.7; 12.99	201.4–296.1
Pupa	Asparagus	0.990	307.7	0.0004	8.4	8.4; 0.137	7.9–8.9	237.0	235.7; 5.579	215.5–255.0
Pupa	Artificial diet	0.994	529.2	0.0002	8.2	8.2; 0.151	7.6–8.7	236.4	236.4; 4.566	220.5–252.5
Egg to egg	Asparagus	0.998	1469.6	<0.0001	7.2	7.2; 0.175	6.5–7.8	800.2	796.3; 17.26	734.8–856.6
Egg to egg	Artificial diet	0.994	355.2	0.0002	7.4	7.4; 0.209	6.6–8.1	671.5	669.2; 23.14	587.9–753.8

Monte Carlo simulation results are presented. All distributions fit a logistic equation; α and β of the logistic, as well as the 95% CIs are presented. For a logistic equation, α = mean.

Table 3. Mean number of days for development (± SE) of larvae, prepupae, and pupae of *C. decolora* reared on asparagus or artificial diet at six temperatures

Temperature (°C)	Food	No. instars (range)	Instar								
			I	II	III	IV	V	VI	Prepupa	Pupa	Total to adult
9.7	Asparagus	5.9 ± 0.3 (5–6)	15.7 ± 0.3 (32)	13.6 ± 0.2 (31)	12.9 ± 0.2 (30)	12.9 ± 0.3 (30)	16.3 ± 0.4 (30)	20.4 ± 0.7 (29)	18.3 ± 0.4 (25)	105.6 ± 0.8 (25)	215.3 ± 1.8 (25)
9.7	Diet	5.3 ± 0.1 (5–7)	14.7 ± 0.3 (41)	11.9 ± 0.1 (41)	11.2 ± 0.2 (41)	13.7 ± 0.3 (41)	14.8 ± 0.7 (27)	16.3 ± 2.0 (7)	23.1 ± 0.6 (15)	107.4 ± 1.4 (15)	199.9 ± 2.0 (15)
14.6	Asparagus	6.0 ± 0.0 (6)	8.7 ± 0.2 (32)	6.8 ± 0.2 (31)	5.8 ± 0.1 (31)	5.8 ± 0.1 (31)	7.6 ± 0.4 (28)	9.3 ± 0.6 (28)	7.4 ± 0.1 (25)	45.0 ± 0.4 (25)	95.4 ± 0.8 (25)
14.6	Diet	5.1 ± 0.1 (5–6)	7.2 ± 0.1 (46)	5.9 ± 0.1 (46)	5.8 ± 0.1 (46)	6.7 ± 0.1 (46)	7.2 ± 0.2 (33)	5.0 ± 1.1 (4)	7.8 ± 0.2 (26)	41.6 ± 0.4 (26)	82.5 ± 0.5 (26)
20.1	Asparagus	5.4 ± 0.1 (4–7)	4.3 ± 0.1 (34)	4.2 ± 0.2 (33)	4.0 ± 0.3 (33)	3.8 ± 0.3 (33)	5.8 ± 0.5 (29)	5.7 ± 0.3 (15)	3.3 ± 0.2 (32)	21.5 ± 0.2 (32)	49.1 ± 0.3 (32)
20.1	Diet	5.0 ± 0.1 (4–6)	3.1 ± 0.1 (47)	3.1 ± 0.1 (46)	3.0 ± 0.1 (46)	3.5 ± 0.1 (46)	4.7 ± 0.3 (39)	3.0 ± 0.0 (1)	4.2 ± 0.2 (33)	20.8 ± 0.2 (33)	41.7 ± 0.3 (33)
24.9	Asparagus	5.3 ± 0.1 (4–7)	3.3 ± 0.1 (29)	2.9 ± 0.1 (29	2.3 ± 0.1 (29)	3.4 ± 0.4 (28)	4.6 ± 0.4 (25)	5.1 ± 0.5 (9)	2.1 ± 0.2 (27)	14.1 ± 0.2 (28)	34.3 ± 0.9 (28)
24.9	Diet	5.0 ± 0.0 (5)	2.0 ± 0.0 (49)	2.0 ± 0.1 (49)	2.0 ± 0.0 (49)	2.1 ± 0.1 (49)	3.4 ± 0.1 (37)	— —	2.5 ± 0.1 (33)	13.9 ± 0. l (33)	27.9 ± 0.2 (33)
29.5	Asparagus	5.6 ± 0.1 (5–6)	2.4 ± 0.1 (52)	2.0 ± 0.1 (52)	1.8 ± 0.1 (52)	2.3 ± 0.1 (51)	2.6 ± 0.2 (45)	4.3 ± 0.4 (24)	1.5 ± 0.1 (15)	11.1 ± 0.1 (15)	26.2 ± 1.1 (15)
29.5	Diet	5.0 ± 0.0 (5)	1.2 ± 0.1 (49)	1.9 ± 0.1 (49)	1.2 ± 0.1 (49)	2.1 ± 0.1 (49)	3.1 ± 0.2 (21)	— —	2.3 ± 0.4 (10)	11.0 ± 0.1 (10)	23.2 ± 0.7 (10)
34.5	Asparagus	— —	2.4 ± 0.2 (17)	1.8 ± 0.1 (13)	2.3 ± 0.3 (3)	— —	— —	— —	— —	— —	— —
34.5	Diet	— —	1.1 ± 0.1 (20)	— —	— —	— —	— —	— —	— —	— —	— —

Data are presented only for individuals that survived through the following instar. *N* is given in parentheses.

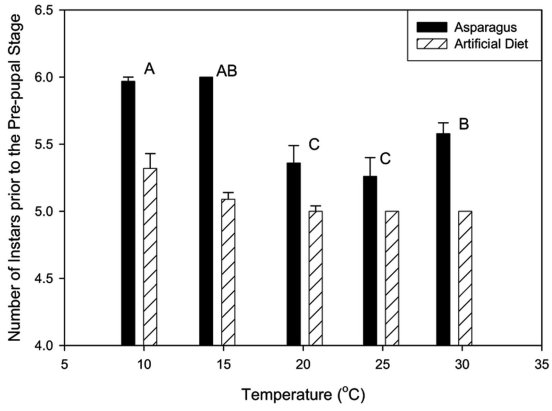

Fig. 1. Effect of temperature and food on the number of instars of *C. decolora.* Temperatures with different letters above the bars are significantly different ($P < 0.05$, Ryan-Einot-Gabriel-Welsch multiple range test).

when larvae were reared on asparagus. The number of instars was intermediate at the high extreme temperature, 29.5°C, and significantly lower at 20.1 and 14.9°C (Fig. 1). The ANOVA model showed a significant temperature effect ($F = 19.31$, df = 4, $P < 0.0001$), a significant food effect ($F = 125.124$, df = 1, $P < 0.0001$), and a significant temperature by food interaction ($F = 5.61$, df = 4, $P = 0.0002$). The interaction term was significant because the number of instars was much more stable among temperatures when *C. decolora* was reared on artificial diet than when they were reared on asparagus (Fig. 1). At all temperatures, *C. decolora* developed through fewer instars when reared on artificial diet (Fig. 1).

The developmental time of individuals from neonate to the end of the pupal stage ranged from 23.2 ± 0.7 d at 29.5°C for larvae reared on artificial diet to 215.3 ± 1.8 d at 9.7°C for larvae reared on asparagus (Table 3). No larvae placed on asparagus when newly hatched developed past the fourth instar at 34.5°C, and no eggs hatched at that temperature. Thirty-five degrees C is above the upper threshold for development of *C. decolora.* The number of days to complete the larval stages declined as temperature increased, and development was more rapid on artificial diet (Fig. 2). Temperature ($F = 4,441.1$, df = 4, $P < 0.0001$) and food ($F = 261.7$, df = 1, $P < 0.0001$) both significantly affected larval development. *C. decolora* required 341.4 DD, above a base temperature of 7.3°C, to complete development from neonate through prepupa on asparagus, whereas 254.5 DD were needed on artificial diet, where the base temperature was 7.7°C (Table 2). The 95% CIs surrounding these estimates, as well as α and β of the logistic distribution, are presented in Table 2.

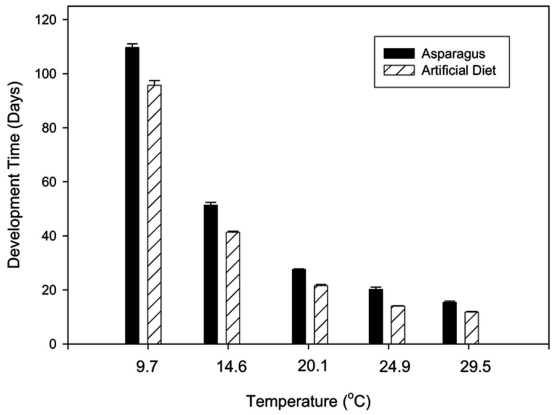

Fig. 2. Effect of temperature and food on development time of *C. decolora* from neonate through prepupa.

Pupae. *Copitarsia decolora* reared on artificial diet had significantly higher pupal weights ($F = 52.24$, df = 4, $P < 0.0001$) than *C. decolora* reared at the same temperatures on asparagus (Table 4). Temperature effects also were significant ($F = 88.40$, df = 1, $P < 0.0001$), with pupae weighing more when reared at lower temperatures. However, no correlation between pupal weight and the number of eggs laid by the emerging females ($F = 0.43$, df = 1, $P = 0.5151$) was observed. Females were significantly heavier than males ($F = 9.43$, df = 1, $P = 0.0023$).

Temperature had a significant effect on the developmental time of pupae ($F = 13,673$, df = 4, $P < 0.0001$; Table 3), with pupae developing more rapidly at higher temperatures. Overall, pupae developed more quickly when the larvae had been reared on artificial diet ($F = 5.89$, df = 1, $P = 0.0160$), but a significant temperature and food interaction was observed ($F = 8.10$, df = 4, $P < 0.0001$). At some temperatures, development of pupae was faster on asparagus and at some temperatures on diet (Table 3). The number of degree-days calculated for pupal development on asparagus was 237.0 using linear regression and 235.7 using @Risk. The 95% CI was estimated between 215.5 and 255.0 DD (Table 2). For pupae that had been reared on artificial diet as larvae, the number of degree-days for development was 236.4 using both regression of the means and @Risk, with a 95% CI of 220.5–252.5 DD.

Velasquez Z. (1988) reported that *C. turbata* completed development from neonate to adult in 55.3 d on onion at 20.4°C. At 20.1°C, we found that *C. decolora* required 49.1 d to complete development through the pupal stage on asparagus. *C. turbata* (probably *C. decolora*) was reported to complete development in 36.1 d on lettuce at 24.5°C (Arce de Hamity and Neder de Roman 1992). We found that development from neonate to adult was 34.3 d on asparagus at 24.9°C. These differences could be caused by differences in host plant quality or to misidentification of the species in the earlier studies because of taxonomic confusion.

Adults. Female moths laid significantly more eggs at 14.6 and 20.1°C (Table 4) than at the other temperatures. The number of eggs per female was significantly lower at 29.5°C. The temperature effect was significant ($F = 18.93$, df = 4, $P < 0.0001$). Although the pupae were larger when *C. decolora* was reared on artificial diet, the females reared on asparagus laid significantly

Table 4. Mean pupal weight, survival (%), no. eggs laid, egg hatch (%), and population growth parameters for *C. decolora* reared on asparagus and artificial diet at six temperatures

Temperature (°C)	Food	Pupal wt (g)	Percent survival to adult	Female longevity (d ± SE)	Male longevity (d ± SE)	Eggs/female (± SE)	Percent eggs hatched	Generation time (d ± SE)	Net reproductive rate (R_0)	Capacity for increase (r_c)
9.7	Asparagus	0.36	71.4	44.4 ± 5.6	44.0 ± 7.3	989 ± 115	0	273 ± 8.8	245.6	0.020
9.7	Diet	0.39	31.9	41.0 ± 10.1	35.2 ± 7.4	507 ± 159	0	257 ± 21.1	56.2	0.016
14.6	Asparagus	0.33	69.4	27.8 ± 2.6	35.5 ± 2.3	1712 ± 184	88.4 ± 1.6	117 ± 5.4	444.3	0.052
14.6	Diet	0.36	55.3	36.3 ± 3.1	32.5 ± 2.7	1223 ± 145	80.9 ± 3.8	103 ± 2.4	247.0	0.062
20.1	Asparagus	0.32	88.9	22.4 ± 1.0	28.1 ± 2.1	1714 ± 140	81.3 ± 5.8	62 ± 4.0	535.4	0.100
20.1	Diet	0.33	66.0	26.3 ± 5.3	27.6 ± 5.0	1547 ± 123	86.1 ± 2.3	51 ± 3.9	332.8	0.135
24.9	Asparagus	0.27	93.3	27.7 ± 8.3	38.7 ± 9.8	879 ± 246	69.9 ± 7.0	45 ± 3.3	294.4	0.125
24.9	Diet	0.33	67.4	24.1 ± 6.3	23.6 ± 5.2	743 ± 94	50.8 ± 15.3	38 ± 2.2	39.0	0.141
29.5	Asparagus	0.26	24.2	11.5 ± 3.2	11.2 ± 2.7	281 ± 67	0	36 ± 1.2	18.2	0.081
29.5	Diet	0.33	20.4	11.3 ± 4.0	41.0 ± 23.0	128 ± 45	0	47 ± 14.1	7.0	0.054
34.5	Asparagus	—	0.0	—	—	—	—	—	—	—
34.5	Diet	—	0.0	—	—	—	—	—	—	—

more eggs ($F = 8.51$, df = 1, $P = 0.0045$). In previous studies, *Copitarsia* sp. females reportedly laid 1,038 eggs when reared on artificial diet (Larrain S. 1996), 572 eggs per female when reared on lettuce (Arce de Hamity and Neder de Roman 1992), and 1,579 eggs per female when reared on onion (Velasquez Z. 1988). Although only 572 eggs were laid on lettuce, the females contained an average of 1,552 ovarioles, suggesting that lettuce is not an ideal host plant for egg maturation.

Survival to the adult stage was high at 9.7°C (71%) and peaked at 24.9°C (93%). Survival fell off rapidly to 25% at 29.5°C, and no insects survived past the fourth instar at 34.5°C. The situation was more complex for eggs. When eggs were laid at room temperature and placed in growth chambers from 9.7 to 34.5°C, percent hatch ranged from 37.6 to 69.5%, with no obvious trend related to temperature (Table 1). No eggs hatched at 34.5°C. When eggs were laid by females reared at the various temperatures, however, percent hatch was higher at 14.6, 20.1, and 24.9°C, and no eggs hatched when laid at 9.7 or 29.5°C. This was most likely not because of temperature effects on egg physiology but rather to the effect of temperature on mating success. The female moths reared at 9.7 and 29.5°C did not have sperm in the spermatheca (R. Simmons, personal communication), indicating that mating did not occur at the more extreme temperatures. When calculating the capacity for increase, we used the percentage egg hatch for eggs laid by females reared at room temperature for the 10 and 30°C treatments.

Intrinsic Rate of Increase. The capacity for increase, r_c, is a function of both insect fecundity and generation time. While the generation time was shorter at 29.5°C than for any other temperature, only 25% of the females survived to the adult stage on asparagus, fecundity was low, and only 53% of the eggs were viable. For *C. decolora* reared on both asparagus and artificial diet, r_c increased from 9.7 to 24.9°C and was much lower at 29.5°C (Fig. 3). The three-parameter modified model of Logan et al. (1976) (Lactin et al. 1995), calculated using mean values of r_c, was significant for asparagus ($F = 66.07$, df = 2, $P = 0.0149$) and artificial diet ($F = 40.54$, df = 2, $P = 0.0242$). The temperature at which population growth ceased (T_{max}) was 31.3°C for asparagus and 30.3°C for artificial diet. The model predicted that population growth reached an optimum at 25.7°C when larvae were reared on asparagus and reached an optimum at 25.0°C when larvae were reared on artificial diet.

Because the three-parameter Logan model does not cross the abscissa, we were unable to estimate a base temperature using that model. We therefore fit a linear regression to the population growth estimates at temperatures below the temperatures that were optimum for population growth. The base temperature was estimated as the temperature at which the regression line crossed the abscissa. For populations developing on asparagus, the base temperature based on regressing mean values was estimated at 6.9°C, and the base temperature on artificial diet was 7.1°C (Fig. 3).

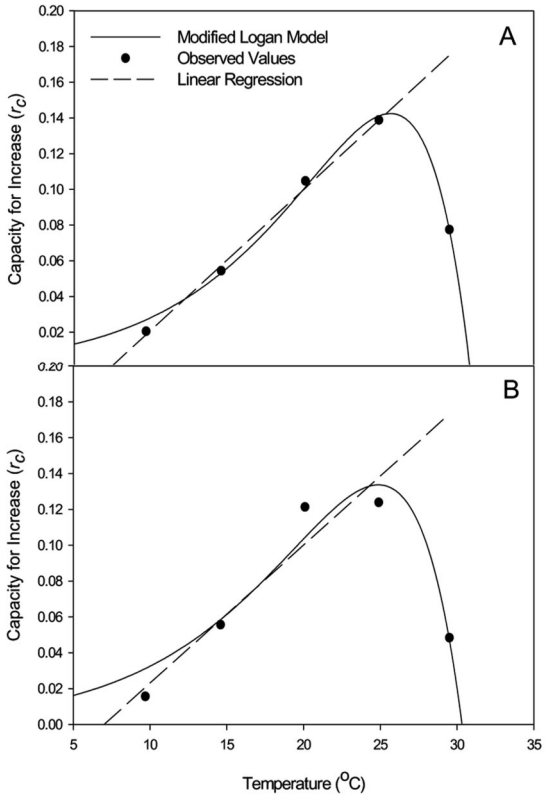

Fig. 3. Effect of temperature on the capacity for *C. decolora* population increase (r_c) when reared on asparagus (A) or artificial diet (B). Linear regression is 10–25°C observations only.

The mean and 95% CIs for T_{max}, the optimum temperature, and base temperature are given in Table 5. The values for population growth on asparagus and artificial diet were quite similar. The values for T_{max} and optimal temperature fit a log logistic distribution with the following parameters: T_{max} on asparagus (γ = 28.92, β = 1.82, α = 8.18), T_{max} on artificial diet (γ = 28.54, β = 1.76, α = 5.68), optimum temperature on asparagus (γ = 22.40, β = 3.21, α = 18.60), and optimum temperature on artificial diet (γ = 16.60, β = 8.39, α = 29.72). The base temperature for population growth on asparagus best fit a Weibull distribution (α = 8.74, β = 4.56), whereas population growth on artificial diet best fit a logistic distribution (α = 7.32, β = 0.54).

Table 5. Estimates of base temperatures, optimum temperatures, and maximum temperatures (T_{max}) for *C. decolora* population growth based on linear and nonlinear models bootstrapped with @Risk

Parameter	Asparagus		Artificial diet	
	Mean	95% CI	Mean	95% CI
T_{max} (°C)	30.8	30.1–31.7	30.4	29.4–31.9
Optimum temperature (°C)	25.6	25.0–26.3	25.0	24.0–26.1
Base temperature (°C)	7.3	6.0–8.3	7.3	5.4–9.2

Example and Conclusion. When assessing the risk posed by *C. decolora*, a critical component will be to determine the likelihood that *C. decolora* eggs could hatch (and the larvae escape) while the commodity travels along its pathway from the field to its final destination. We conducted a preliminary pathway analysis to show the importance of estimating a range of values for base temperature and degree-days rather than relying on the standard regression approach. This example is designed only to show the importance of including estimates of variability in risk analysis and includes some simplifying assumptions.

Let us assume that asparagus with *C. decolora* eggs is harvested immediately after eggs are laid. It is placed in coolers at temperatures well below the developmental threshold for egg development. The asparagus is shipped to the United States, where some is discarded at the warehouse. We assume that the asparagus with *C. decolora* eggs is discarded in a dumpster (rather than being ground in a compactor or garbage disposal) when ambient temperatures average 17°C. Using the mean values for base temperature and degree-days, 9.2 DD are accumulated each day. We assume that warehouses have trash pickup at least once per week and that the trash is compacted, incinerated, or buried in a landfill. Consequently, larvae would need to escape during the week in the dumpster or they would be killed when the asparagus is destroyed. Under this scenario, using mean values for base temperature and degree-days, the eggs would accumulate only 64.4 DD, while it takes them 69.1 DD to hatch. We would calculate, therefore, that there is no risk.

What if we use the distribution of values rather than the mean? We entered the functions for base temperature and degree-days into @Risk and sampled from these distributions 10,000 times using Latin Hypercube sampling. At each iteration, @Risk determined whether or not the number of degree-days accumulated in the field exceeded the number required for egg hatch. In most of the cases, it was predicted that no egg hatch would occur. However, there was an estimated 2% chance that one or more eggs would hatch. Depending on the quantity of asparagus, the number of *C. decolora* eggs and the probability that a larva could find a host plant, 2% hatch may or may not be considered above the threshold of acceptable risk. Using the range of values for development allows one to make more informed decisions regarding the risk associated with pest species.

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